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Poplar vulnerability to xylem cavitation acclimates to drier soil conditions

Hosam Awad[a,b], Tete Barigah[a,b], Eric Badel[a,b], Herve Cochard[a,b] and Stephane Herbette[a,b,*]

[a]Clermont Université, Université Blaise Pascal, UMR 547 PIAF, F-63177, Aubière, France
[b]INRA, UMR 547 PIAF, F-63100 Clermont-Ferrand, France

Correspondence
*Corresponding author,
e-mail: stephane.herbette@
univ-bpclermont.fr

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Xylem vulnerability to cavitation differs between tree species according to their drought resistance, more xerophilous species being more resistant to xylem cavitation. Variability in xylem vulnerability to cavitation is also found within species, especially between in situ populations. The origin of this variability has not been clearly identified. Here we analyzed the response of xylem hydraulic traits of *Populus tremula* × *Populus alba* trees to three different soil water regimes. Stem xylem vulnerability was scored as the xylem water potential causing 12, 50 and 88% loss of conductivity (P_{12}, P_{50} and P_{88}). Vulnerability to cavitation was found to acclimate to growing conditions under different levels of soil water content, with P_{50} values of −1.82, −2.03 and −2.45 MPa in well-watered, moderately water-stressed and severely water-stressed poplars, respectively. The value of P_{12}, the xylem tension at which cavitation begins, was correlated with the lowest value of midday leaf water potential (ψm) experienced by each plant, the difference between the two parameters being approximately 0.5 MPa, consistent with the absence of any difference in embolism level between the different water treatments. These results support the hypothesis that vulnerability to cavitation is a critical trait for resistance to drought. The decrease in vulnerability to cavitation under growing conditions of soil drought was correlated with decreased vessel diameter, increased vessel wall thickness and a stronger bordered pit field $(t/b)^2$. The links between these parameters are discussed.

Introduction

The summer drought and heat wave that occurred in Europe in 2003 seriously affected forest ecosystems (Levinson and Waple 2004, Meehl and Tebaldi 2004, Rebetez et al. 2006). Visible impact was reported in several regions of France, from partial crown dieback to individual deaths (Bréda et al. 2004, Rozenberg and Pâques 2004). As a consequence, there has been a rising demand for more drought-resistant plant materials, and this demand will surely increase with the greater frequency and intensity of drought episodes expected in the future. Detailed knowledge of the mechanisms of drought response may give new insights into factors controlling plant productivity and survival in drought-prone regions (Brodribb and Hill 1999, Brodribb et al. 2002, Nardini and Salleo 2005). The mechanisms of trees' drought response are very diverse. Trees may adapt or acclimate to drier conditions. The first process occurs through gradual natural selection of genotypes with greater fitness in more xeric habitats. These ecotypes

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Abbreviations – ψ_m, midday leaf water potential; ψ_p, predawn leaf water potential; C, control plants; MS, moderately water-stressed plants; P_{12}, P_{50} and P_{88}, xylem water potential causing 12, 50 and 88% loss of conductivity; SS, severely water-stressed plants.

could be identified in marginal populations and find use in future breeding or reforestation programs. In contrast, drought acclimation is a phenotypic response to a variation in water regime, whereby each individual tree modifies its phenotype during its lifespan. Before proposing drought-tolerant genotypes to foresters it is important to document the ability of current genotypes to acclimate to drier conditions.

During the last two decades, research on xylem embolism has considerably improved our understanding of tree responses to drought. In trees, water is transported under tension (negative pressure) in the xylem vessels. Under drought conditions, the tension in the xylem conduits increases and cavitation can occur. Cavitation causes an embolism, which restricts the water supply to leaves and other organs. It occurs only when the xylem pressure drops below a specific threshold value (ψ_{cav}) related to pit wall porosity (Tyree and Sperry 1988). Xylem vulnerability to cavitation is correlated with drought tolerance (Maherali et al. 2004, Pockman and Sperry 2000, Tyree et al. 2003), more xerophilous species being more resistant to xylem cavitation. This suggests that species able to keep xylem vessels functional under extreme droughts can more readily survive such events. Vulnerability to xylem cavitation has also been found to vary substantially within species (Lopez et al. 2005). For some species, these variations have been associated with a genotypic variability (Cochard et al. 2007, Ennajeh et al. 2008). For others, xylem vulnerability to cavitation has also been shown to acclimate to environmental conditions such as irradiance (Barigah et al. 2006, Cochard et al. 1999) or soil nutrient availability (Harvey and Van Den Driessche 1999). However, ability to acclimate to drier soil conditions remains largely unexplored and has been restricted to drought-tolerant species (Beikircher and Mayr 2009, Ladjal et al. 2005). Only a slight increase in xylem vulnerability to cavitation was observed in response to drought for a drought-sensitive willow cultivar (Wikberg and Ögren 2007). Responses to drought are species-specific and depend on the plant's hydraulic strategy (Bréda et al. 2006). For example, only one of three Mediterranean cedar species tested showed an acclimation of its vulnerability to cavitation to drier soil conditions (Ladjal et al. 2005).

In this study, we analyzed the capacity of xylem hydraulic traits in poplar to acclimate to different soil water regimes. Poplar is a pioneer species that is very sensitive to water stress and highly vulnerable to cavitation (Cochard et al. 2007). Pioneer species are known to acclimate better to changed environments (Bazzaz 1979, Fetcher et al. 1983, Grime 1979). Thus we hypothesized that it would display a marked plasticity in its vulnerability to cavitation. Potted poplar clones were grown in a controlled environment under different level of water stress and the impact on their hydraulic traits and xylem properties was analyzed at the end of the growth period. We discuss the trade-off between safety and efficiency.

Materials and methods

Plant material and culture conditions

Experiments were carried out on a hybrid poplar (*P. tremula* × *P. alba*, clone INRA 717-1B4). Plants were multiplied clonally in vitro on Murashige and Skoog medium (Murashige and Skoog 1962). When they reached 4 cm in height, they were gradually acclimated on a hydroponic solution (Morizet and Mingeau 1976) and grown in a controlled environment room: 16-h daylight, at 21–22°C, 40 μmol m^{-2} s^{-1} (day) and 18–19°C (night) with relative humidity 70 ± 10%. At age 57 days and height 30 cm, they were transferred to 10-l pots filled with a commercial soil (40% black, 30% brown and 30% blond peat moss, pH 6.1, DUMONA-RN 75-3851 Arandon, Holland) and grown in a greenhouse: 16-h daylight, at 22(±1)°C, 350 μmol m^{-2} s^{-1} (day) and 19(±1)°C (night) with relative humidity 70 ± 10%. The same weight of soil was provided so that the weight of each pot was 5 kg. Watering was then adjusted until each pot weighed 7 kg.

Experimental design

The experiment started at the date of the potting. Twenty-four poplar plants were divided into three sets of eight plants subjected to three different water regimes. The first set of plants was used as a control (C) and was maintained with optimal water status, i.e. 70–100% of field capacity (FC) between successive waterings. The second set of plants was moderately water-stressed (MS) so that the soil water content ranged between 40 and 75% of FC. The third set of plants was severely water-stressed (SS) so that the soil water content ranged between 25 and 45% of FC. Leaf wilt was observed when the soil content reached 25% of FC. The soil water content was checked by weighing the pots. At the start of the experiment, each pot weighed 7 kg and each plant was at optimal water status. The plants were then watered every 3, 4 or 5 days depending on their assigned watering regime. Fig. 1 shows the time course of the FC of the soil. For each set of plants, the watering was performed when the minimal soil water content (25, 40 or 70 % of FC) was reached in one pot, and the water was brought using a

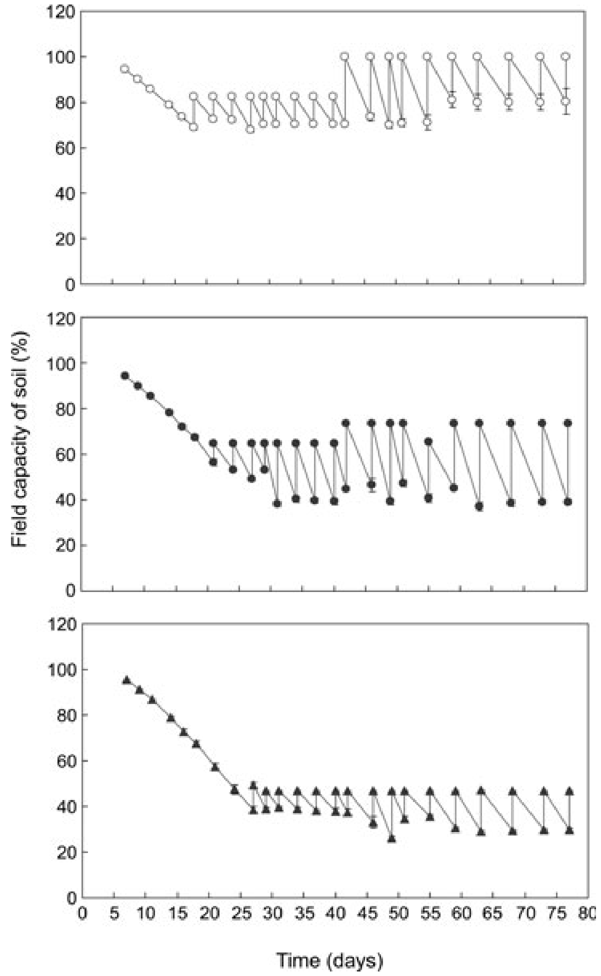

Fig. 1. Time course of the FC of the soil under three different water regimes. A survey of the FC of the soil was carried out for C plants (open circles), MS plants (closed circles) and SS plants (closed triangles). When the FC reached the minimal value (see section on Materials and methods), pots were watered to adjust FC to the maximal value. Each point represents the mean value (±SE) of the FC for eight plants.

watering can to reach the maximal soil water content (45, 75, 100% of FC).

Leaf water potentials

The midday and predawn leaf water potentials (ψ_m and ψ_p) were measured using a pressure chamber (Scholander et al. 1965). Two leaves per plant were removed to measure ψ_m and ψ_p. Predawn water potential was recorded between 04:00 and 06:00 solar time and ψ_m was recorded between 12:00 and 14:00 solar time. The measurements were made at 46, 47, 80 and 81 days after the beginning of the experiment, just before watering (Days 46 and 80) and 1 day after watering (Days 47 and 81).

Native embolism and specific conductivity

Native embolism (% of loss conductivity) and specific conductivity (mol MPa^{-1} m^{-1} s^{-1}) were measured on 0.2-m long samples using a XYL'EM® xylem embolism meter (Bronkhorst, Montigny-les-Cormeilles, France), following the procedure described previously (Cruiziat et al. 2002, Sperry et al. 1988). The technique involves measuring the hydraulic conductance of segments before and after water refilling (K_i and K_{max}, respectively). Stem segments were excised under water and their ends cut with a sharp razor blade. The basal cut end was then attached to the hydraulic apparatus. The solution used was composed of 10 m*M* KCl and 1 m*M* $CaCl_2$. The solution flowed from a flask through the branch segment, which was kept under water during the measurement. We measured K_i and K_{max} under low pressure (6 kPa). Before measuring K_{max}, air obstructing stem xylem vessels was removed by applying a series of 5-min hydraulic pressure flushes (0.15 MPa).

Vulnerability curves

Vulnerability to xylem cavitation was assessed using the Cavitron technique (Cochard 2002a, Cochard et al. 2005). Its principle is as follows: a centrifugal force increases the water tension in a xylem segment and the loss of hydraulic conductance is measured at the same time. The curve of percentage loss of xylem conductance (PLC) vs xylem water tension represents the vulnerability to cavitation of the sample. Vulnerability curves were plotted on one 0.28-m long sample per plant, i.e. eight samples for each watering rate. Xylem pressure (P) was first set to a reference pressure (−0.5 MPa) and the maximal conductance (K_{max}) of the sample was determined. The xylem pressure was then set to a more negative value for 3 min and the conductance (K) of the sample was again determined. The percent loss of conductance of the sample was then given by:

$$\mathrm{PLC} = 100 \times (1 - K/K_{max}) \quad (1)$$

The procedure was repeated for more negative pressures (with −0.25 or −0.5 MPa increments) until PLC reached at least 90%. Rotor velocity was monitored with an electronic tachymeter (10 rpm resolution). The PLC curves were fitted using the following sigmoid function (Pammenter and van der Willigen 1998):

$$\mathrm{PLC} = 100/\left(1 + e^{(s(P-P_{50})/25)}\right) \quad (2)$$

where xylem water potential causing 50% loss of conductivity (P_{50}) is the pressure causing 50% loss of hydraulic conductivity and s is the slope of the curve at this point (MPa^{-1}). Eqn (2) was used to estimate xylem water potential causing 12 and 88% loss of conductivity (P_{12} and P_{88}) values. $P_{12} = P_{50} + 50/s$, we call it the 'air entry point' (Sparks and Black 1999). It is interpreted as the xylem tension level at which runaway cavitation and embolism begin when the resistance to the air entry of pit membranes within the conducting xylem is overcame (Tyree and Sperry 1988). $P_{88} = P_{50} - 50/s$, the 'full embolism point', is interpreted as the limiting tension before the xylem becomes totally non-conductive (Domec and Gartner 2001). In our study, P_{12} and P_{88} were defined as the capacities for maintaining xylem conductivity. The more negative the P_{12} and P_{88} values are, the higher is the capacity to maintain xylem hydraulic conductivity.

Wood infradensity

Wood density is defined as:

$$d = \frac{M_0}{V_s} \tag{3}$$

A 2-cm long segment was cut from one end of each sample. Its fresh volume (V_s) was measured using an analytical balance by the Archimedes principle of water displacement. The dry mass (M_0) was determined after one night in a gravity convection oven at 104°C.

Anatomical traits

Anatomical traits were determined on the samples used to measure vulnerability to cavitation. For each sample, six cross sections were prepared from the basal part of the sample and stained with Astra blue and Safranin dyes. They were examined under an optical microscope (Zeiss Axioplan 2, Zeiss, Jena, Germany) and three images per cross section were randomly recorded using a digital camera (AxioCam HR, Zeiss) and AXIOVISION DIGITAL IMAGING software. After spatial calibration, anatomical measurements were made by image analysis using IMAGEJ software (Rasband 1997–2009). Two spatial magnifications were used. On ×20 images (1 pixel = 0.52 µm), the vessels were isolated by automatic segmentation (Ridler 1978). Their diameters (µm), their density (number mm^{-2}) and the total area they occupy on the image (μm^2) were measured. Then, on ×40 images (1 pixel = 0.26 µm), we measured the intervessel wall thickness (t) (µm) and the conduit wall span (b) (µm) to calculate the bordered pit field strengthening parameter $(t/b)^2$, according to Hacke et al. (2001). For these thickness measurements, the error is estimated to 0.26 µm. It was repeated 10 to 15 times for each wall in order to evaluate the repeatability.

Results

Three sets of poplar plants were subjected to three contrasting water regimes (Fig. 1) and a survey of leaf water potentials was conducted. Before watering, the SS plants showed lower ψ_p and ψ_m values than the other plants (Fig. 2). After watering, there was no significant difference between the three treatments for ψ_p, and SS plants had the highest ψ_m values. No difference was observed between control (C) and MS plants, except for the ψ_p value, which was lower for MS plants before watering on Day 80.

At the end of the experiment, several physiological and anatomical parameters were analyzed (Table 1). The growth in height of the SS plants was reduced compared with C plants. The three sets showed differences in vulnerability to cavitation (Table 1 and Fig. 3). The SS plants appeared to be the least vulnerable to cavitation, with the lowest P_{50} values, whereas the C plants appeared to be the most vulnerable, with the highest P_{50} values. A significant difference was also found for P_{12} and P_{88} values between the SS plants and the plants from the other treatments. However, the slopes of the vulnerability curves were similar (Fig. 3 and Table 1). No significant difference was found in specific conductivity between the three sets of plants, or for embolism level, which remained low. At the anatomical level, vessel diameters and hydraulic diameters were smaller in the

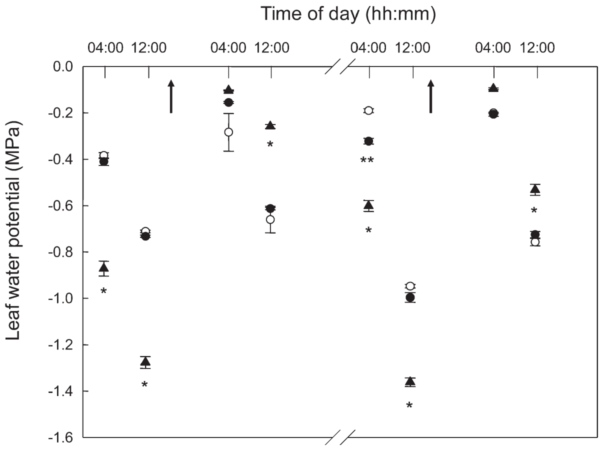

Fig. 2. Time course of leaf water potentials (ψ) of poplars depending on water regime. The ψ values were measured on C plants (open circles), MS plants (closed circles) and SS plants (closed triangles) at two periods separated by a break on the axis: 46–47 days (left) and 80–81 days (right) after the beginning of the treatment. The ψ_p were recorded at 04:00 solar time and the ψ_m were recorded at 12:00 solar time. The waterings are indicated with an arrow. The measurements were made just before watering and the day after watering. Each data represents the mean value (±SE) for eight plants. Data that are significantly different between treatments have different symbols (*, **).

Table 1. Physiological and anatomical parameters in poplar stems grown under three different water regimes. P_{50}, xylem pressure causing 50% loss of hydraulic conductivity; P_{12}, xylem pressure causing 12% loss of hydraulic conductivity; P_{88}, xylem pressure causing 88% loss of hydraulic conductivity; A_v, total surface area occupied by vessels; $(t/b)^2$, vessel wall thickness (t) conduit wall span (b). Data represent the mean values (±SE) for eight plants. Values on each line not followed by the same letter differ significantly at $P \leq 0.05$ (one-way ANOVA)

Parameter	Well-watered plants	Moderately water-stressed plants	Severely water-stressed plants
Plant height (cm)	148 ± 2^a	141 ± 2^a	117 ± 2^b
P_{50} (MPa)	-1.82 ± 0.05^a	-2.03 ± 0.06^b	-2.45 ± 0.09^c
P_{12} (MPa)	-1.44 ± 0.10^a	-1.57 ± 0.12^a	-1.95 ± 0.14^b
P_{88} (MPa)	-2.20 ± 0.05^a	-2.50 ± 0.05^b	-2.95 ± 0.09^c
Slope line (% MPa^{-1})	158 ± 32^a	125 ± 17^a	120 ± 23^a
Specific conductivity (mmol m^{-1} MPa^{-1} s^{-1})	1.63 ± 0.22^a	2.05 ± 0.15^a	1.53 ± 0.08^a
Embolism level (%)	20.2 ± 6.3^a	12.0 ± 7.5^a	7.0 ± 2.5^a
Wood density (g l^{-1})	371 ± 9^{ab}	354 ± 4^a	382 ± 8^b
Vessel diameter (μm)	48.3 ± 0.7^a	46.7 ± 0.7^a	41.6 ± 0.8^b
A_v (μm^2)	18.3 ± 0.6^a	18.7 ± 0.4^a	19.4 ± 0.5^a
Vessel density (number mm^{-2})	94 ± 3^a	103 ± 4^a	135 ± 3^b
Vessel wall thickness (μm)	3.89 ± 0.03^a	4.10 ± 0.04^a	4.53 ± 0.11^b
$(t/b)^2$	0.0046 ± 0.0005^a	0.0032 ± 0.0002^a	0.0085 ± 0.0007^b

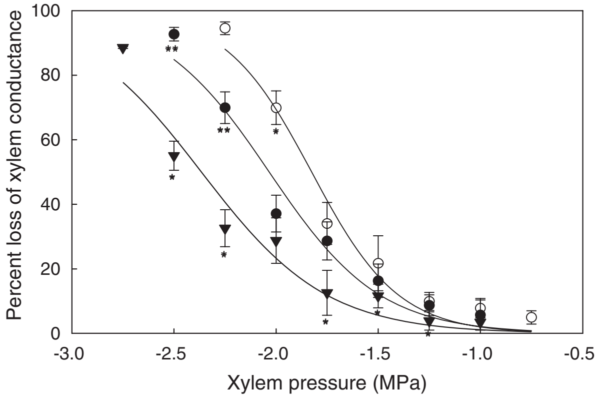

Fig. 3. Xylem vulnerability curves of stems depending on water regime. The percentage loss of xylem hydraulic conductance with decreasing xylem water potential is represented for C plants (open circles), MS plants (closed circles) and SS plants (closed triangles). Each data represents the mean (±SE) of eight samples. Full lines represent the fitted data according to Eqn (2) (see section on Materials and methods). Data that are significantly different between treatments have different symbols (*, **).

SS plants than in the MS and C plants. Also, SS plants had the largest vessel densities and the thickest vessel walls. There was no significant difference in the stem area occupied by vessels (A_v) between the plant sets.

The correlation between vulnerability to cavitation and anatomical traits was tested. Fig. 4 shows that the P_{50} was not correlated with wood density. Also, the linear regression between P_{50} and wood density values for each plant was not significant ($r = 0.351$ and $P = 0.1189$). On the other hand, P_{50} was positively correlated with vessel diameter and negatively correlated with vessel wall thickness (Fig. 4). The plants that were most resistant to cavitation also had the highest values of $(t/b)^2$.

Discussion

Poplars are well known for their susceptibility to drought and are among the most vulnerable trees tested to date (Hacke and Sauter 1996). Cochard et al. (2007) investigated the differences in drought resistance among some poplar clones, with small differences up to 0.12 MPa. Here, we show that the resistance to drought can vary between poplar plants from the same genotype exposed to different water soil availabilities, with differences up to 0.63 MPa. These results suggest that phenotypic plasticity accounts for a large part of the within-species variability for vulnerability to cavitation. The observed acclimation of vulnerability to cavitation to soil water content supports the hypothesis that cavitation resistance is a trait for drought resistance across trees.

Difference in water regimes

ψ_p and ψ_m have been considered as good indices for evaluating plant water status (Shackel et al. 1997). The three sets of trees truly underwent three different water regimes because they showed significantly different ψ_p values before watering. Control plants kept their ψ_p values constant before and after watering. This indicates that the water availability did not vary for these plants in the course of the experiment. MS plants did not experience water stress, as revealed by the absence of significant difference for ψ_m and for growth between MS and C plants (Table 1). However, MS plants probably adjusted their water loss from the leaves without any

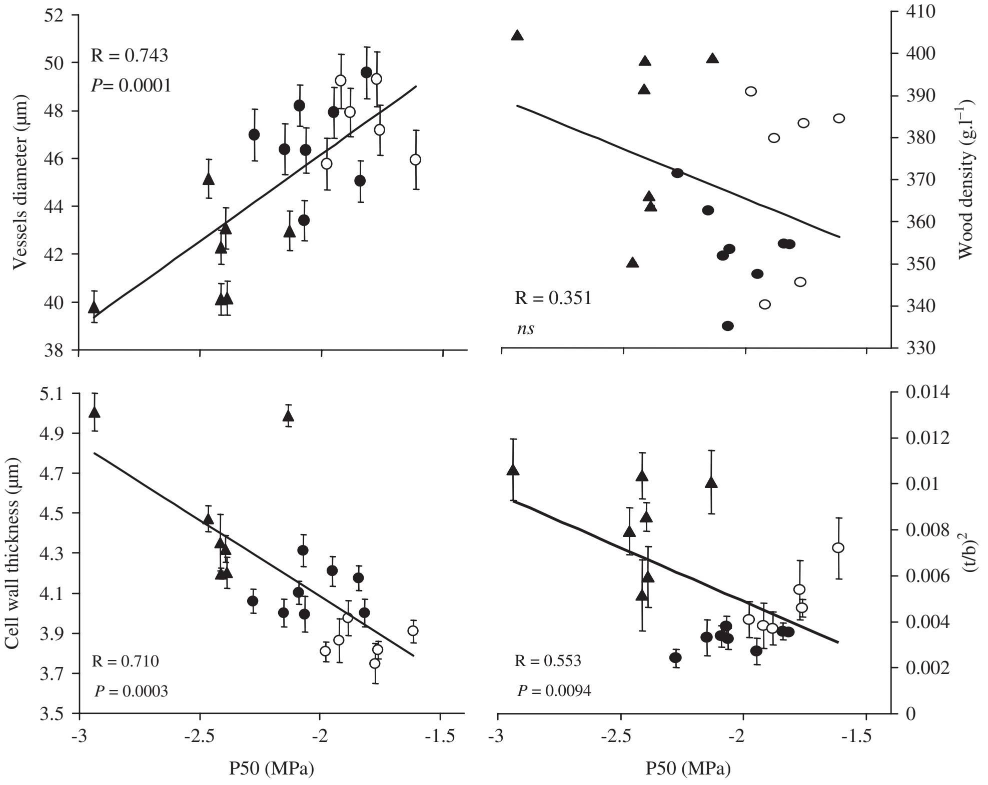

Fig. 4. Correlation between xylem pressure causing 50% loss of conductivity (P_{50}) with vessel diameter (top left), vessel wall thickness (bottom left), wood density (top right) and $(t/b)^2$ (bottom right). Each point represents the data for one individual tree from C plants (open circles), MS plants (closed circles) or SS plants (closed triangles). For vessel diameter, vessel wall thickness and $(t/b)^2$, each data point is a mean (±SE) of 92 to 167 measures on three stem sections. The line is a linear regression, statistically significant with the P value indicated. The linear regression is not significant (ns) with $P = 0.1189$ for wood density plotted vs P_{50}.

change in their stem conductivity or xylem structure (vessel diameter, A_v, vessel density; Table 1). The slower decrease in soil water content of MS plants (0.304 l day^{-1} at the end of the treatment) between successive waterings suggests lower water consumption compared with C plants (0.385 l day^{-1}, see also Fig. 1). On the contrary, SS plants experienced water stress; both their ψ_m and ψ_p were lower before watering and their growth was reduced. Thus, this experimental set-up allows us to document the effect of water soil availability on vulnerability to cavitation, with or without water stress.

Variation in vulnerability to cavitation

Here, we found that the vulnerability to xylem cavitation acclimated to a decrease in soil water availability. No difference for native steady xylem embolism was found between the three water regimes. We can therefore rule out the possibility that the drought-induced decrease in vulnerability to cavitation was artificially because of an increase in the embolism level. If water-stressed plants have higher level of embolism, then the vulnerability curves would be plotted on the remaining functional vessels, which are the most resistant. In this study, it was then essential to observe similar levels of embolism across treatments to decipher true acclimation from more mechanical shifts in xylem vulnerability curves. The magnitudes of these changes in vulnerability to cavitation were linked to the severity of the water stress, and they were observed even when the poplar trees did not experience water stress, the MS plants being less vulnerable to cavitation than the C plants. It is well known that stomatal control occurs to prevent xylem cavitation during drought (Sack and Holbrook 2006). The interval between ψ_{leaf} when the stomata close and ψ_{leaf} when the xylem is embolized is known as 'the safety margin' (Brodribb and Holbrook 2004, Sperry 2004, Sperry et al. 2002). The interval between the value of P_{12} (Table 1) and the lowest ψ_m value experienced by each plant set (Fig. 2) remained stable (around 0.5 MPa) for the three sets of plants. Although stomatal closure allows xylem cavitation to be prevented or delayed, it is detrimental for gas exchanges and so may be the main control for short-term drought or mild water shortage. By contrast, adjustment of vulnerability to cavitation is a long-term process, implying the formation of new vessels, and can protect the plant from the next wave of cavitation events during long-term drought. In agreement with our results, some studies report a relationship between the xylem vulnerability to cavitation of stems and the ψ_m value experienced by plants (Brodribb and Cochard 2009, Cochard 2002b, Cochard et al. 2002, Hacke et al. 2000).

Xylem vulnerability to cavitation is thought to be a critical trait for drought resistance as it is correlated with drought resistance of different species (Maherali et al. 2004, Pockman and Sperry 2000, Tyree et al. 2003). Vulnerability to cavitation has also been found to differ between genotypes from the same species (Cochard et al. 2007, Dalla-Salda et al. 2009, Pita et al. 2003, Sangsing et al. 2004). However, the relationship between this variability and drought tolerance is still unclear. The decrease in vulnerability to cavitation when water deprivation occurs strongly supports the hypothesis that it is a trait for drought tolerance. To further test this hypothesis, the trees that grew under the three water regimes should be tested for their ability to withstand a new severe drought, which could be applied by stopping watering until the xylem water potential reaches the P_{88} value of the C plants.

Hydraulic compensation and trade-offs

Both hydraulic conductivity and drought-induced vulnerability to cavitation depend on pit membrane connecting xylem vessels. Thus resistance to cavitation has been assumed to be accompanied by lower pore hydraulic conductivity, and ultimately stem hydraulic conductivity (Sperry and Hacke 2004, Zimmermann 1983). This classic idea of trade-off between efficiency and safety functions is largely based on interspecific comparisons. Our data do not support it. Water shortage causes variation of vulnerability to cavitation but no change in the hydraulic conductivity. This lack of trade-off has already been observed at the within-species level for sequoia and Scots pine trees (Burgess et al. 2006, Martinez-Vilalta et al. 2009). However, this is less surprising in conifers because of the role of torus-margo pits in preventing cavitation (Cochard 2006). Although no difference was observed for stem hydraulic conductivity, vessel diameter, which accounts for the hydraulic conductivity of vessels, is positively correlated with vulnerability to cavitation (Fig. 4). Hence, we can suppose that the pit membrane conductivity is higher in the trees that appear less vulnerable to cavitation to compensate for a reduced diameter. This conflicts with the efficiency-safety trade-off based on the pit membrane.

The negative water pressure in the xylem causes two threats: cavitation events through air seeding and xylem collapse. Among the anatomical traits we measured, vessel diameter, vessel wall thickness and strengthening of the bordered pit field $(t/b)^2$ were correlated with vulnerability to cavitation. The correlation we found between $(t/b)^2$ and P_{50} is weaker than those found at the between species level by Hacke et al. (2001). This can easily be explained by the small P_{50} and $(t/b)^2$ ranges we found at the within-species level compared with this other study. In addition, $(t/b)^2$ data were not different between the C and MS plants, weakening the correlation between P_{50} and $(t/b)^2$. This suggest that $(t/b)^2$ may be less sensitive to water regimes than vulnerability to cavitation. It was suggested that the $(t/b)^2$was a safety factor for conduit collapse by negative pressure (Hacke et al. 2001). Although there is no causal link between vulnerability to cavitation and $(t/b)^2$, as they are located in different wall regions, the two traits are linked because they depend on the xylem pressure.

Wood density was proposed as an accessible parameter to estimate vulnerability to cavitation, based on investigations between species (Hacke et al. 2001). In this within-species investigation, no such correlation was evident (Fig. 4). Also, the water regimes did not lead to any difference in wood density (Table 1). Similarly, Cochard et al. (2007) did not find any correlation when comparing poplar clones or willows. In addition, there is no deterministic link between wood density and vulnerability to cavitation that is based on the pit membrane. Thus, it seems unrealistic to use wood density as a measure of vulnerability to cavitation at the within-species level.

In conclusion, vulnerability to cavitation becomes significantly lower as water soil content decreases, especially with a scaling of the air entry point (P_{12}) according to the ψ_m value. This supports the hypothesis that vulnerability to cavitation is a critical trait for resistance to drought. This study also shows the utility for poplar wood production in the light of predicted climate changes. It should be possible to adjust water supply to improve cavitation resistance. Easily measurable parameters such as vessel diameter, vessel wall thickness or $(t/b)^2$ are relevant anatomical traits that could be used to assess vulnerability to cavitation of a poplar genotype under different growth conditions.

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